

Spine deficiency and polymorphism in a population of *Gasterosteus aculeatus*: an adaptation to predators?

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A population of *Gasterosteus aculeatus* from a muskeg lake on the Queen Charlotte Islands shows a spine polymorphism, with 80% lacking the second dorsal spine and 68% lacking the pelvic spines. Females were more prevalent among phenotypes with greater spine number, and males were more common among those with fewer spines. Adult females, as well as juveniles of both sexes with pelvic spines, were more frequent in the limnetic habitat, whereas adult males and juveniles without pelvic spines were common in the littoral region.

Five species of piscivorous birds, each in low numbers, foraged in the lake. Extensive predation in the limnetic region by *Gavia immer* and, secondarily, *Podiceps* spp. is implicated as a selective pressure favouring the greater spined phenotype.

Odonate nymphs (*Aeshna* spp.) consumed juvenile fish in predation experiments and in the lake proper. Nymphs were common in the littoral zone, where submerged debris provided substrate for foraging. It is proposed that spine loss in this population of *G. aculeatus* is an adaptation to the hunting technique of *Aeshna*, whereby reduced external structures such as spines minimize frictional contact for a grappling predator. Experimental data and other gasterosteid populations are discussed with reference to these proposals.

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On a constaté l'existence d'un certain polymorphisme chez une population de *Gasterosteus aculeatus* d'un lac marécageux des îles de la Reine Charlotte: chez 80% des poissons, il n'y a pas de seconde épine dorsale et chez 68%, les épines pelviennes sont absentes. Chez les poissons qui ont le plus grand nombre d'épines, ce sont surtout les femelles qui prédominent, alors que chez les poissons dont le nombre d'épines est réduit, ce sont surtout les mâles qui prédominent. Les femelles adultes et les jeunes des deux sexes qui portent des épines pelviennes se retrouvent surtout en habitat limnétique, alors que les jeunes sans épines pelviennes habitent surtout la région littorale.

Cinq espèces d'oiseaux piscivores, toutes en nombre assez réduit, se nourrissent dans le lac. La prédation importante dans la région limnétique par *Gavia immer* et, à un degré moindre, par *Podiceps* spp., opère une pression sélective qui avantage le phénotype à épines nombreuses.

Au cours d'expériences et en nature, dans le lac même, les larves d'odonates (*Aeshna* spp.) se sont avérées prédatrices des petits poissons. Les larves abondent dans la zone littorale où des débris submergés constituent un substrat propice à la prédation. Il est possible que la perte des épines chez cette population de *G. aculeatus* soit une adaptation aux techniques de chasse d'*Aeshna*, adaptation qui réduit les structures externes, telles que les épines, de façon à minimiser pour ce genre de prédateur le contact par friction. Les résultats de cette étude et la comparaison avec d'autres populations de gasterostéidés sont examinés en fonction de cette hypothèse.

[Traduit par le journal]

Introduction

Spine-deficient populations of the threespine stickleback (*Gasterosteus aculeatus*) are uncommon within the circumboreal distribution of the species. Four such polymorphic populations are known from the Queen Charlotte Islands, British Columbia (54°N, 132°W) (Moodie and Reimchen 1973), one from Texada Island (49°40' N, 124°28' W) (Bell 1974; Larsen 1976), and several from the

Outer Hebrides, U.K. (N. Giles, personal communication). Parallel trends in spine loss have also been documented from a Pliocene assemblage of *G. doryssus* in Nevada, U.S.A. (Bell 1974), and in populations of the brook stickleback (*Culaea inconstans*) and ninespine stickleback (*Pungitius pungitius*) from central Canada (Nelson 1969, 1971).

Spine polymorphisms have a genetic basis (Nelson 1977) and show stability in frequencies over time (Bell 1974). Each of the extant North American populations is believed to be independently derived from fully spined parental stock following

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the Wisconsin glaciation (Moodie and Reimchen 1976a; Nelson 1977).

Selective mechanisms responsible for spine reduction are not understood. The principal environmental correlate among many of these populations is an absence or reduced number of predatory fish (see Bell (1976) for review). Various explanations have been proposed for the widespread loss of "useless characters" in animal populations, including energy conservation (Barr 1968) and molecular noise suppression (Regal 1977). Spine-deficient phenotypes may initially accrue an increased fitness through diversion of energy requirements from production of bone, muscle, and nerve tissue to reproductive demands. However, these interpretations may overlook immediate morphological advantages to spine loss. Nelson (1969), in a discussion of pelvic deficient populations of *Culaea inconstans*, suggested an advantage of reduced weight and streamlining for efficient escape responses in dense vegetation.

The present study examines a spine polymorphism in a population of *G. aculeatus* from the Queen Charlotte Islands, with particular emphasis on distribution of phenotypes and hunting techniques of several predators. From the data, inferences are made on the maintenance of variability and on advantages to spine reduction. Other parameters of this population, including feeding habits, parasitism, and pigmentation patterns, will be considered separately (Reimchen, in preparation). General measurements on meristic characters such as lateral scutes, gill rakers, and vertebrae have been described elsewhere (Moodie and Reimchen 1976b).

Study area

Boulton Lake (53°47' N, 132°06' W) is located in an area of low-lying muskeg and coniferous forest (elevation 60 m) on Graham Island, the largest and most northerly in the Queen Charlotte archipelago (Fig. 1). The lake (18 ha) is fed principally by groundwater seepage, and has an intermittent outlet draining to marine waters 8 km to the northwest. The substrate is a thick organic ooze in the southern half of the lake and fine gravel in the central and northern regions. Numerous partially decayed root systems, small logs, and hummocks of soft mud characterize the littoral zone. Most of these roots and trunks are still *in situ* and presumably reflect an historical shoreline and reduced water levels. Overhanging growth of *Sphagnum* occurs along the shoreline and in some cases extends 1.5 m onto the lake surface. Floating and submerged vegetation is

common and includes an approximate 10% cover by *Nuphar luteum* and locally abundant *Scirpus subterminalis*.

Common macroinvertebrates are trichopteran larvae (Phryganeidae), odonate nymphs (Aeshnidae, Cordulidae, Coenagruidae), leeches (Hirudidae), and occasional adult diving beetles (Dytiscidae).

Gasterosteus aculeatus is the only fish species in the lake. Many of the surrounding watersheds have well developed outlet streams and contain a number of species including *Salmo clarkii*, *Salvelinus malma*, *Oncorhynchus* spp., as well as *G. aculeatus*.

Methods

Collections of fish were made over a 10-year period on the following dates: July 1969, May–June 1970, September 1970, June 1971, October–December 1975, August–December 1976, February–December 1977, and January–December 1978. Within the periods from 1975 to 1978, the lake was usually visited once a week for collecting and general observations on bird activity. Depth contours were determined from four transects of the lake, with measurements made to the nearest 0.1 m.

A variety of collecting techniques was employed, the efficiency of each varying with the nature of the bottom. Along most of the lakeshore, standard sized minnow traps (6.3-mm mesh) were used. These traps are size selective, capturing adults and subadults greater than 35 mm. Most juveniles were collected with a beach seine (mesh 3 mm²) in a 100-m stretch of the west shore, the only area in the lake shallows lacking obstructions. In 1977, a trawl (width 5 m, depth 3 m, length 8 m, coddend 2 mm mesh), towed behind a boat, was used for sampling the central area of the lake. Due to shallow water, the mouth of the trawl extended through the entire water column, and thus pelagic and benthic fish were not distinguishable in the samples. Stationary minnow traps were suspended at 0.5 m beneath the surface, at midwater, and on the bottom. Of these, only the bottom traps yielded large numbers of fish ($N = 632$). Although stickleback were commonly seen near the surface, they were rarely captured ($N = 25$) in the midwater or surface traps.

To provide some indication of possible phenotype selectivity from capture techniques, an enlarged passive trapping system was constructed using fine mesh screen. Fish which moved along the shore were channelled into the large enclosure. Sex and phenotype frequencies were similar to those caught in shoreline minnow traps and seine.

The majority of fish retained were placed in 50% formaldehyde and later transferred to a 10% solution. Standard length was measured with vernier calipers, and the sex was recorded (gonads of juveniles were stained with methylene blue for identification). Presence or absence of each dorsal, pelvic, and anal spine was verified under a dissecting microscope. For a detailed description of the spines and support structures, 130 fish were stained and cleared with the alizerin–trypsin method (Taylor 1967).

Spines are not expressed during the first month after hatching; apices initially protrude from beneath the epidermis on individuals about 10 mm in length, and by 15 mm, the spines are exposed. The full complement of spines consists of three anterior to the dorsal fin, two on the pelvis, and a small spine slightly anterior to the anal fin.

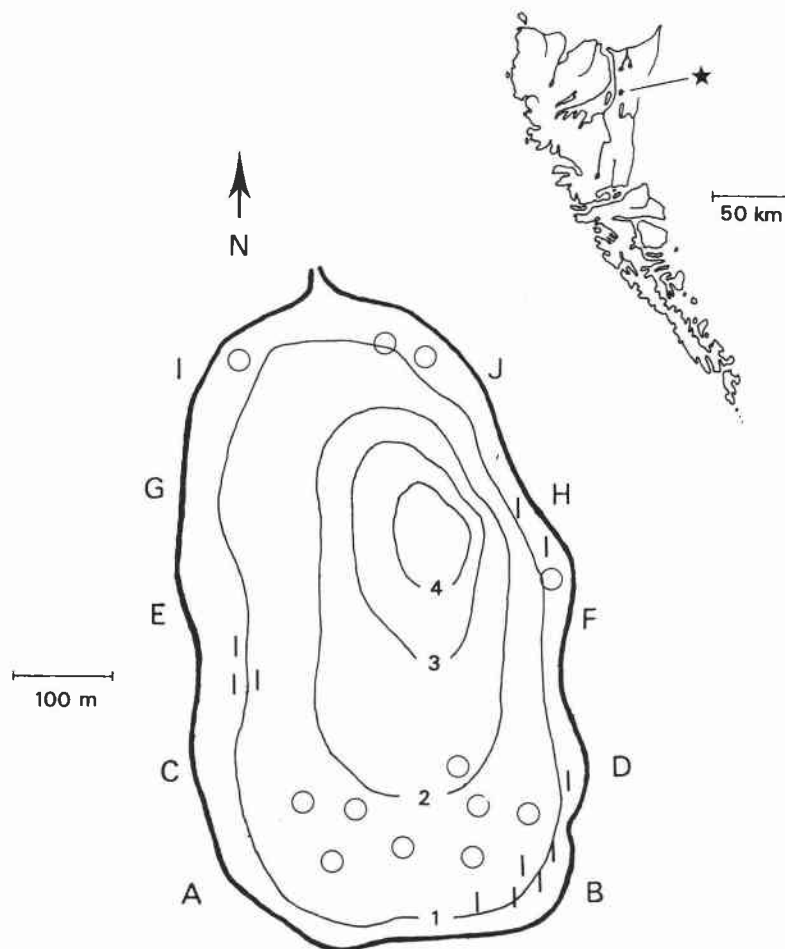


FIG. 1. Boulton Lake showing depth contours (in metres), *Nuphar* (circles), and generalized distribution of *Scirpus* (vertical lines). Depth measurements made at 50-m intervals on transects A-B, C-D, E-F, etc. Inset, Queen Charlotte Islands.

For presentation of data, phenotypes were classified according to expression of the large spines, i.e. D-10 (first dorsal present, second dorsal absent), P-II (both pelvic spines present), P-00 (both pelvics absent), etc. Variations in the small spines (third dorsal and anal) were not included in this classification.

On each visit to the lake, records were kept of the occurrence, abundance, and distribution of piscivorous birds. With some species, more detailed observations were made on diving durations and types of food obtained using a 20–45 \times spotting scope.

Odonate nymphs were collected from the lake and kept in aquaria for predation experiments with the stickleback. To determine preferences for prey size, 10 nymphs in each of three tanks were offered different size classes of fish (15–25 mm, 30–40 mm, 50–60 mm); numbers consumed were recorded on successive days. Further comparisons were made to determine the survival of two phenotypic classes (least spined: D-10/P-00; and greater spined: D-II/P-II, D-II/P-10, D-II/P-00, D-10/P-II and D-10/P-10). About 15 fish (15–25 mm) with similar proportions of the two classes were placed in a tank with five nymphs (35–45 mm). When about 50% had been eaten, the survivors were removed and scored; this was replicated seven times. Similar experiments were carried out in screened enclosures (0.5 m³) within the lake. Each aquarium and enclosure contained a small water-saturated tree branch to provide a substrate for the

nymphs. The size of these experiments was limited by the inability to capture large numbers of juvenile fish without injury incurred from seining or handling.

During these experiments, observations were made on the hunting techniques of the odonates. Information on their lake distribution was collected during trap settings for stickleback, as well as with benthic trawls. Seventy nymphs collected throughout the year were dissected and scored for stomach contents.

Results

Phenotype description and abundance

First, second, and third dorsals were absent with frequencies of 0.03, 80.0, and 2.3% respectively. Loss of the second dorsal was correlated with a size reduction of the associated pterigiophore and a slight posterior displacement of the first dorsal from its normal position (Fig. 2A). Absence of the third dorsal was more frequent among individuals lacking the second dorsal than among those with the second dorsal present ($\chi^2_{(1)} = 13.7, P < 0.001$).

The pelvis showed extensive variation in girdle

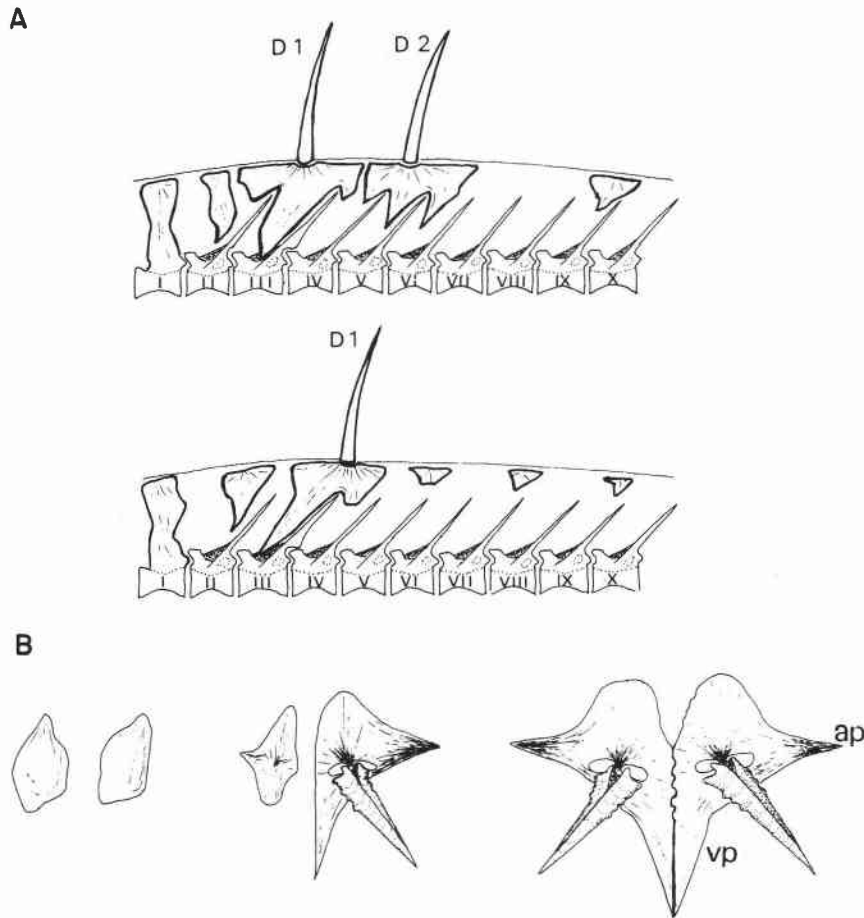


FIG. 2. Variation in dorsal and pelvic skeletal elements. (A) Dorsal spine phenotypes and associated support bones. First dorsal (D1) and second dorsal (D2) shown in common positional relationship to specific vertebra (numbered). Categories referred to in text include D-II (upper figure) and D-I0 (lower figure). (B) Pelvic girdle and spine phenotypes. Categories include P-00 (left), P-I0 (center), and P-II (right). *vp*, ventral plate; *ap*, ascending process. Representative specimens were drawn but skeletal material was highly variable.

and spine morphology, from virtual absence, except for two reduced elements of the ventral shield (65%), to one-half pelvis (15%), through to complete expression (20%) (Fig. 2B). Well developed spines were present with a complete ventral shield and ascending process, whereas reduced or minute spines occasionally occurred with a partially developed shield. Directional asymmetry was observed in the intermediate phenotypes; of 1401 fish with one-half pelvis, 77% had the shield and spine on the left side of the body. There were no distinct associations between absence of pelvic spines and loss of the second dorsal ($\chi^2_{(2)} = 3.13$, $P = 0.21$).

The least spined of the phenotypes, lacking the second dorsal and pelvis, was most frequent, representing 50% of the population. Fully spined individuals were uncommon, occurring with a grand mean of 4.3%. Although the frequencies have fluctuated

over the sampling period, the broad pattern of abundance has remained similar (Table 1).

Consistent differences in sex ratio were evident among some of the phenotypes. Females were more common among individuals with both large dorsals and among those with both pelvic spines, whereas males were in a large excess only in the single dorsal-no-pelvis condition (Table 2). Thus, females dominate the greater spined phenotypes and males the least spined. This relationship is further exemplified when individuals are ranked according to total spine number, including the presence or absence of the third dorsal and anal spines (Fig. 3).

Habitat distribution

There were seasonal and age-related differences in the distribution of the fish. Fry appear in late May

TABLE 1. Percentages of major phenotypes between 1969 and 1978. Individuals categorized according to presence or absence of second dorsal (i.e. D-II or D-I0) and of pelvic spines (i.e. P-II, P-I0, or P-00). Fish less than 20 mm length excluded

Year	Sample size	Phenotypes					
		D-II, P-II	D-II, P-I0	D-II, P-00	D-I0, P-II	D-I0, P-I0	D-I0, P-00
1969	174	5.8	1.7	14.9	4.6	6.9	66.1
1970	2582	3.9	3.8	18.6	8.8	11.1	53.9
1971	199	1.5	2.0	14.6	14.6	8.0	59.3
1975	786	3.8	2.7	13.2	15.0	12.5	52.8
1976	1460	5.5	5.1	13.6	13.7	12.9	49.3
1977	2095	5.0	3.5	13.9	17.0	13.2	47.4
1978	1798	3.6	3.1	16.2	11.2	9.1	56.7
Total	9094	Mean 4.3	3.6	15.6	12.6	11.4	52.5

TABLE 2. Frequencies of each sex within spine phenotypes (juveniles excluded)

	Sample size	Phenotype					
		D-II, P-II	D-II, P-I0	D-II, P-00	D-I0, P-II	D-I0, P-I0	D-I0, P-00
Male	4131	34.7	39.0	39.4	48.6	55.1	59.9
Female	3972	65.3	61.0	60.6	51.4	44.9	40.1

$\chi^2_{(5)}$ on raw numbers = 234.4, $P < 0.001$

and frequent shallow areas of the lake shore, under or near submerged logs and overhanging banks, and in *Scirpus* stands. Young of the year were not detected in the central parts of the lake until late August, and by October large numbers were present. During winter months and throughout the following year, this cohort appears to be primarily in open water and in *Nuphar* beds some distance from shore. In April and May, approximately 22 months after hatching, the cohort has reached adult size (50 mm) and moves to the lake shore for reproduction.

There was some partitioning of the lake habitat between sexes, with an excess of adult males (50+ mm) near shore and an excess of females (40+ mm) in open water (Fig. 4). In addition, sub-adult males (40–50 mm) were more frequent in *Nuphar* beds. Juveniles less than 40 mm had an equal sex ratio in both shoreline and open-water habitats. The predominance of territorial males in the littoral zone would be expected during the spring and summer reproductive season. However, lakeshore samples obtained from autumn and winter months showed a similar excess of males, whereas open-water habitats had an equal sex ratio (Fig. 5).

There were indications of a vertical stratification of the sexes in open water regions. Collections from the trawl, which sampled the entire water column,

showed, in adults, an excess of females (as in Fig. 4). Small numbers captured with stationary traps in midwater and surface positions had a similar trend (females, 72%; $N = 25$); however, samples from benthic traps had an equal sex ratio and, in several cases, an excess of males (Fig. 5). Examination of stomach contents of the fish (in progress) shows more pelagic food items in the female and more benthos in the male.

Frequencies of the spine phenotypes differed between habitats in the lake. Preliminary investigations of this population in 1970, using only littoral fish, indicated major differences in phenotype frequencies between juveniles and adults. Individuals with both pelvic spines were uncommon (4%) in young-of-the-year fish (15–25 mm), but abundant (25%) in adults. Fish with full dorsals were common in fry (30%), rare in the 30–50 mm length class (8%), and again, common in adults (25%). Although selective elimination was implicated from these shoreline samples, subsequent collecting of juveniles from the limnetic region suggests, rather, a differential movement of the phenotypes after hatching. Fish with pelvic spines, of both sexes, were more common in open water than near shore. The differences are significant among fish less than 40 mm (male, $\chi^2_{(1)} = 61.5$, $P < 0.001$; female, $\chi^2_{(1)} = 58.9$, $P < 0.001$), but not among larger fish (male, $\chi^2_{(1)} = 0.57$, $P = 0.45$; female, $\chi^2_{(1)} =$

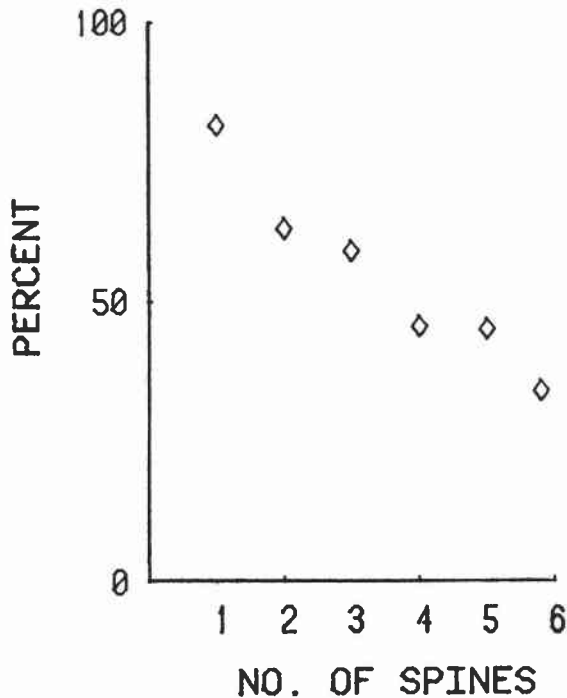


FIG. 3. Association between sexes and total spine number. Triangles show percentage of males for each spine category (males + females = 100%). $N = 37, 376, 4202, 1889, 1261, 338$ for spine categories 1 to 6.

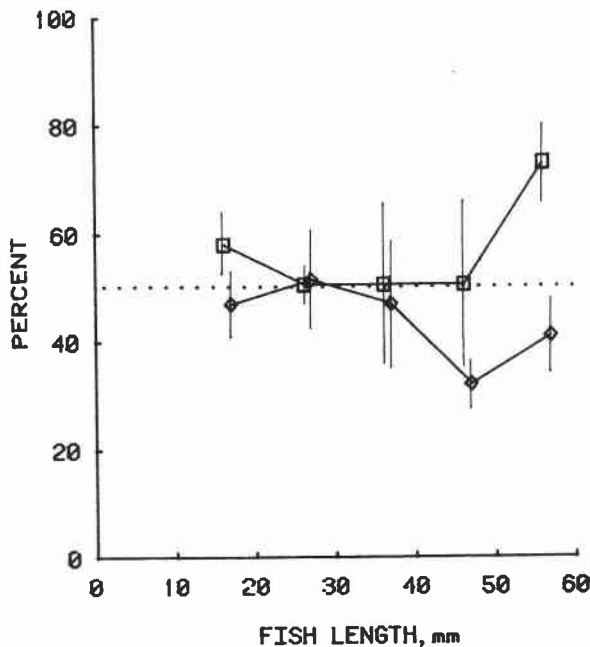


FIG. 4. Percentage of males in relation to length class and habitat. \square , shoreline; \diamond , open water. Dotted line shows equal sex ratio. All samples from 1977. Vertical line = one standard deviation.

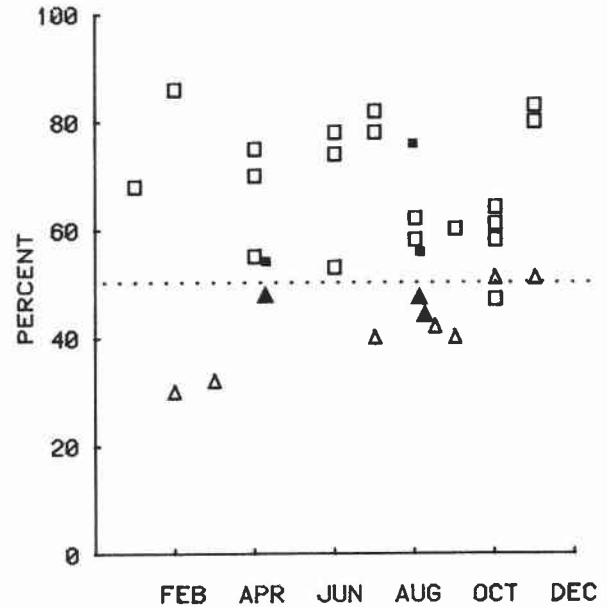


FIG. 5. Percentage of adult males (>50 mm) for month and habitat. \square , shoreline samples; \triangle , open-water samples; \blacksquare , benthic samples from *Nuphar* stands; \blacktriangle , benthic samples from open water. Dotted line shows equal sex ratio.

0.18, $P = 0.69$). Habitat associations of the six phenotypes (combinations of dorsals and pelvics) are shown for three length classes and both sexes (Fig. 6). The smallest fish (less than 20 mm), although primarily near shore, show the greatest difference in phenotype frequencies between littoral and limnetic habitats. The fully spined phenotype (D-II/P-II) in males was about 10 times, and in females, about 5 times, more frequent in open water than in shoreline positions, both of these being statistically significant (Table 3). The least spined phenotype (D-10/P-00), conversely, was significantly more common near shore. Intermediate length classes (20–40 mm), rare in shoreline habitats, showed similar trends, although significant values were present only in D-10/P-10 and D-10/P-00 males and D-II/P-00 females. Among larger fish (greater than 40 mm), each phenotype was equally distributed between open water and shoreline, in both sexes.

To summarize, individuals showing the greater spine expression were most prevalent in open water regions in spring and summer, whereas those with the least spine complement occurred near shore. These differences are a combination of three distinct components: (1) adult females tended to be more spined than males, as well as more frequent in open water, whereas males predominated in benthic and shoreline positions; (2) among subadults of both sexes, phenotypes with pelvic spines were

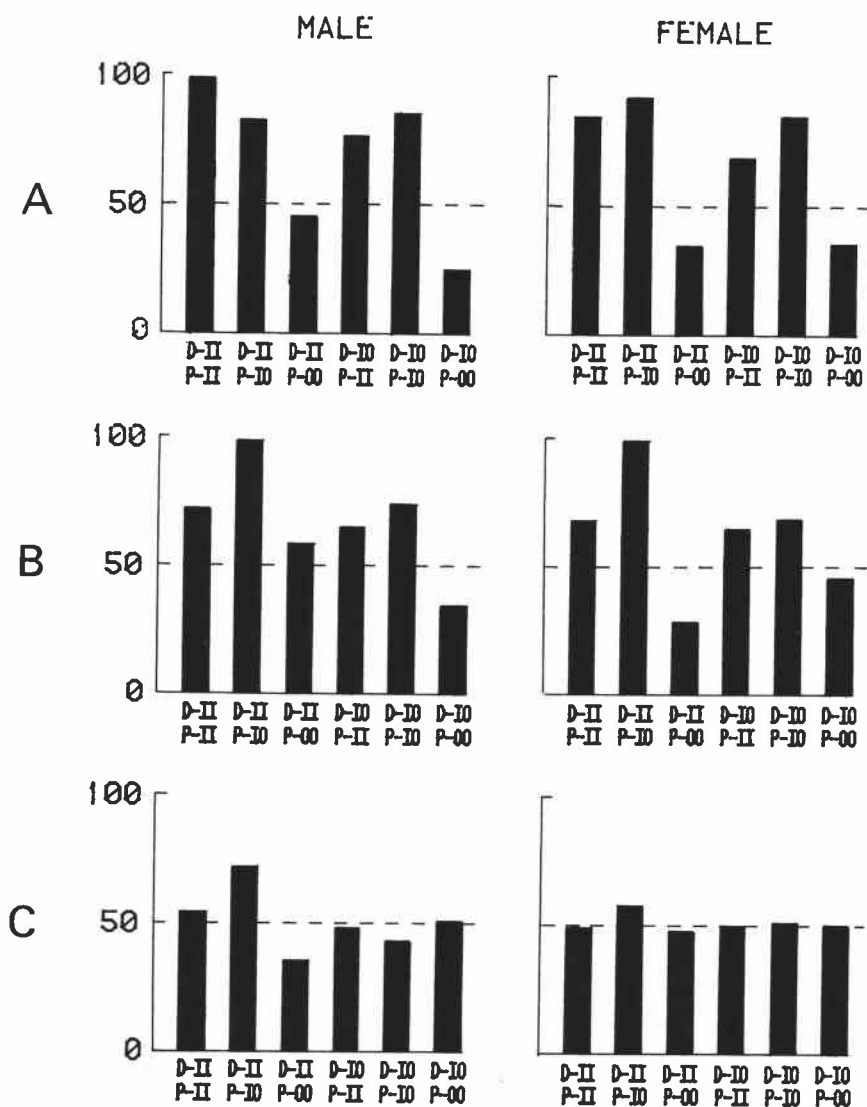


FIG. 6. Summary of habitat associations between phenotypes. Vertical axis represents percentage of a specific phenotype in open water in comparison to total numbers of that phenotype captured (open water + shoreline). Horizontal dashed line at 50% indicates an equal distribution between habitats. (A) 15–20 mm fish. (B) 20–40 mm fish. (C) 40–60 mm fish. For statistical analysis and sample sizes refer to Table 3. Samples collected in 1977 with trawl in open water, and seine and minnow traps in shoreline habitat.

more abundant in open water and those without pelvics were more common near shore; (3) small juveniles (less than 15 mm), all without spine expression, were primarily found near shore.

Predators

Seven species of piscivorous birds were seen on the lake during the study: common loon (*Gavia immer*), red-necked grebe (*Podiceps grisegena*), horned grebe (*P. auritus*), common merganser (*Mergus merganser*), red-breasted merganser (*M. serrator*), hooded merganser (*Lophodytes cucullatus*), and belted kingfisher (*Megasceryle alcyon*).

The loon and kingfisher were resident from March to September, and the remaining species occurred irregularly from August through March (Table 4).

A pair of common loons, which regularly nest on the lake, appeared to be the major predators on adult fish. The loons foraged up to 13 h per day when feeding young, and in all exchanges, stickleback constituted the only prey species. In one 4-h period of continuous observation, some 35 adult-size stickleback were fed to the chick. Parental feeding continues for 6 to 8 weeks, after which adults and fledglings move to marine waters.

When foraging for its own requirements, the

TABLE 3. Sample sizes and probabilities (corrected χ^2 analysis) of phenotype distribution between open water and shoreline habitats as represented in Fig. 7. Samples collected with trawl in open water, and seine and traps in shoreline habitats. N = sample size

Length class, mm	Sex	Shore, N	Central, N	Phenotype					
				D-II, P-II	D-II, P-I0	D-II, P-00	D-I0, P-II	D-I0, P-I0	D-I0, P-00
15-20	♂	151	33	0.001*	0.333*	0.476*	0.003*	0.001	0.009
	♀	116	48	0.021*	0.032*	0.219	0.168	0.012	0.112
20-40	♂	60	333	0.315*	0.374*	0.298*	0.219	0.025	0.024
	♀	47	298	0.298*	0.095*	0.023	0.305	0.201	0.504
40-60	♂	355	181	0.974	0.110	0.145	0.868	0.168	0.369
	♀	235	305	0.982	0.642	0.769	0.979	0.774	0.983

*When expected values are <5, Fisher's exact probability is given.

TABLE 4. Occurrence of diving birds on Boulton Lake. Data summarized from all years of observation

Species	Month											Days occurring per month	Maximum observed per day	
	J*	F	M	A	M	J	J	A	S	O	N*			D†
<i>Gavia immer</i>				x	x	x	x	x	x				30	1-3
<i>Podiceps grisegena</i>		x	x						x	x	x		5-15	1-2
<i>P. auritus</i>		x	x						x	x			10	2
<i>Mergus merganser</i>			x						x	x			5	10
<i>M. serrator</i>			x						x	x			3	4
<i>Lophodytes cucullatus</i>									x	x	x		5	1
<i>Megaceryle alcyon</i>			x	x	x	x	x	x	x				30	1-2

*Variable littoral ice cover.
†Complete ice cover.

adult generally swallows its prey beneath the surface, and it is therefore difficult to obtain direct values on the quantity of prey consumed. It is known that piscivorous birds require about 20% of their body weight in food per day (Van Dobben 1952; Robertson²); hence for a common loon (weight 2500 g), this would total 500 g daily. If it fed exclusively on adult stickleback (mean weight 1.2 g), 417 fish would be consumed. During the 6-month residency, one loon would take 75 060 fish. This estimate will be conservative if the loon is taking smaller size classes or foraging more extensively when feeding the young. Conversely, the value could be lower if food requirements are less than 20%, or if alternate food items are obtained. It is apparent that this predator constitutes a significant source of fish mortality. Diving activity was predominantly in the limnetic habitat; of 269 sightings, 76% occurred in water greater than 2 m in depth and 95% more than 30 m from shore (Fig. 7). The distribution broadly coincides with the major habitat of adult female stickleback and the 25-50 mm length class. There was, correspond-

ingly, little overlap with the macrobenthos, young-of-the-year stickleback, or territorial adult males.

Predation by one or, occasionally, two kingfishers was common throughout spring and summer. Of 40 successful captures seen at close range, only adult fish were taken. Assuming that energy requirements are 20% of body weight (Tjornlid 1973), a kingfisher (weight 150 g) would consume 25 adult stickleback per day, and about 5250 fish during the 7-month residency. This represents only 7% of the numbers captured by the loon.

Foraging by the kingfisher was restricted to within 15 m of shoreline and was most extensive where suitable perching trees occurred and where the bottom gradient was gently sloping. This area of the lake is dominated by adult male stickleback in spring and summer.

The remaining species of diving birds occurred in low numbers, alternating with visits to other lakes and marine waters. Grebes and hooded mergansers foraged extensively during these visits, but common and red-breasted mergansers dove infrequently. These species encountered different length and age classes of prey than did the loon and kingfisher. In late fall and winter months, young of

²Robertson, L. 1971. Predation by fish-eating birds on stocks of Pacific herring, *Clupea larengus*, in the Gulf Islands of British Columbia. Report of the Pacific Biological Station, Nanaimo, B.C.

the year have reached a size of 20–30 mm and are found throughout the lake. The majority of breeding adults (50+ mm) have disappeared, either from predation or other mortality. Data on foraging distribution for these birds are less extensive than for the loon, but there are general differences among the species. The horned grebe, smallest of the divers, was observed on four occasions in *Scirpus* stands taking young-of-the-year fish. The red-necked grebe occurred in open water (15 sightings) and in *Nuphar* beds (3 sightings), and in each case was seen capturing subadults (40–50 mm). The hooded merganser (three sightings) was seen in the same area taking young of the year as well as subadults. Increasing ice cover in the littoral zone during November and December restricted all foraging to open-water regions.

Another source of mortality in the fish was macroinvertebrates, primarily dragonfly nymphs (*Aeshna palmata* and *A. eremita*). Final instars of these species attain lengths of 40–45 mm and are active stalking predators, taking invertebrates as well as small fish (Pritchard 1964, 1965). Distribution, assessed from minnow traps and benthic trawl, showed *Aeshna* to be rare or absent in the central parts of the lake but abundant near shore (Fig. 7). In this region they were frequently found near overhanging banks, on submerged logs, and within eroded hummocks. Examination of the digestive tract of 70 nymphs yielded integument and skeletal remains of juvenile stickleback in 8 individuals, dipteran and trichopteran larvae in 17, and unidentified remains in 45.

In aquaria, nymphs deprived of food for 7 days immediately began stalking fish that were introduced, and usually within a few minutes would have captured a fish. When presented with different length classes, nymphs showed distinct preferences for the smallest individuals, each consuming an average of 1.8 fish per day (Table 5). Both stalking behaviour and attacks on adult fish (50+ mm) were rare, even when alternate food items were not available. In several tanks, nymphs were kept with adult fish for several months and no predation occurred. There were behavioural differences between juveniles and adults in their response to the nymphs, which suggest interactions in the lake. Young-of-the-year fish would move away from a stalking nymph and not readily approach a stationary one, whereas adults showed no such behaviour, often hovering adjacent to the nymphs.

After observing a number of successful attacks on the fish, it seemed plausible that defensive adaptations to this predator would be very different from those of a diving bird. *Aeshna* are active visual

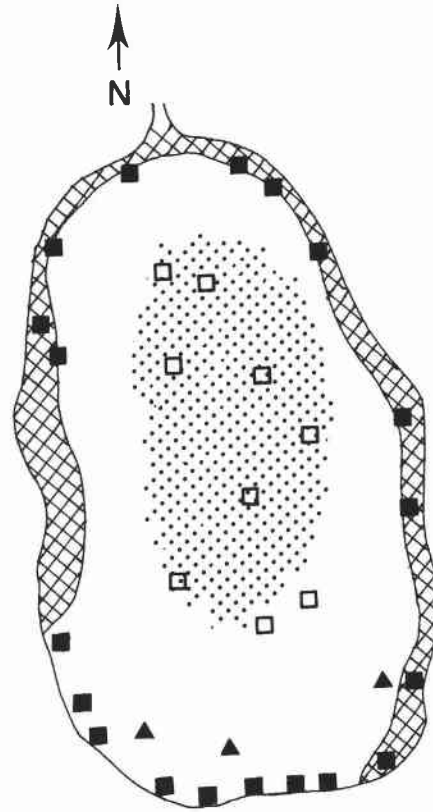


FIG. 7. General distribution of some predators. *G. immer* (dotted) and *M. alcyon* (hatched) showing areas where diving was observed. Relative abundance of *Aeshna*: ■, common; ▲, occasional; □, absent. Observations summarized from all years. Depth contours given in Fig. 1.

TABLE 5. Summarized results of predation experiments with *Aeshna* and different size classes of fish. The experiment was run for 25 days, and all fish were replaced every 6 days with new groups (10 fish per length class)

Tank	Numbers eaten		
	15–25 mm	30–40 mm	50–60 mm
A	30	1	1
B	28	3	0
C	30	0	0
% of total	97.8	4.4	1.1

predators with attacks elicited primarily by prey movement (Pritchard 1965; personal observation). In aquaria, they were frequently seen moving to the top of submerged logs and stalking juvenile fish (15–25 mm) which foraged or sheltered in the vicinity. When the nymph was within 10 mm of the prey, the labium was rapidly extended and the fish was seized with sharp labial palps, most frequently on the ventral body surface (Fig. 8). The labium

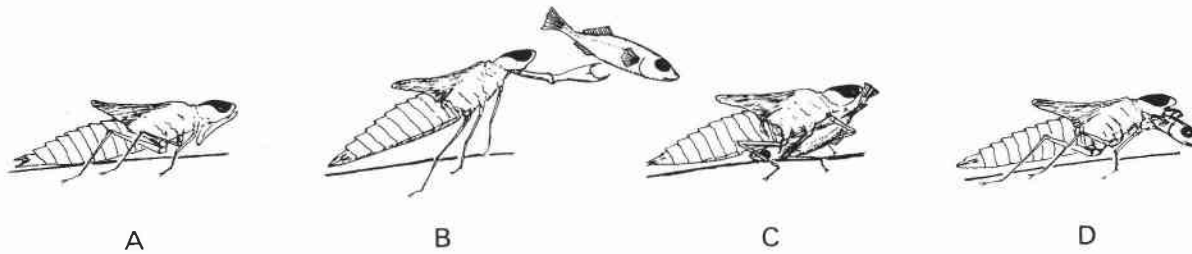


FIG. 8. Stalking and prey capture by *Aeshna*. (A) Approach. (B) Attack. (C) Restraint of fish. (D) Ingestion.

was then retracted with the prey and held close to the mouthparts, and prey was progressively chewed and ingested. I noted in these attacks that the presence of spines on the fish would not necessarily reduce the probability of capture nor increase the likelihood of escape.

In the six attacks observed on slightly larger fish (30 mm), the nymphs exhibited a slight variation on this capture technique. Fish were seized on the ventral body surface, but thereafter, nymphs had difficulty restraining the rapid body movements. In these situations, the nymph moved its forelegs around the body of the fish and restrained many of the escape motions (Fig. 8C). Gripping of the smooth fish body may be enhanced by two rows of minute spines on the tibia and by tarsal claws. Similar to attacks on smaller fish, spines seemed to offer no defense against this predator. Indeed, it was evident that the presence of either dorsal or pelvic spines could represent a small but significant disadvantage to the fish since they would provide the nymph with external structures for grasping and frictional contact.

Predation experiments have not detected any significant differences or trends in mortality among spine phenotypes. In total, the nymphs took 93 of 155 greater spined and 142 of 253 least spined ($\chi^2_{(1)} = 0.0$).

Discussion

The degree of spine loss in the Boulton Lake population represents an unusual morphological divergence within the circumboreal distribution of *G. aculeatus* (Hagen and Gilbertson 1972; Moodie and Reimchen 1976b; Gross 1978). However, the range of spine expression and frequencies is similar to a spine-deficient population of *G. aculeatus* from Paxton Lake, Texada Island (Bell 1974; J. D. McPhail, personal communication). In each locality, one large dorsal spine is normally missing; in Paxton it is the first dorsal spine (50%), and in Boulton it is the second dorsal spine (80%). The pelvic girdle ranges from absence (Paxton 60%, Boulton 65%) to full expression, with bilateral

asymmetry and intermediate states common. Similar variation of the pelvis was observed in spine-deficient populations of *Culaea inconstans* (Nelson 1969; Nelson and Atton 1971). These parallel trends are suggestive of a common selective regime undergoing directional change towards total absence of spines or a balanced polymorphism.

The data that have emerged from this study show sexual dimorphism in spines and habitat differences between the sexes and spine phenotypes. Individuals with greater spine expression were primarily limnetic in spring and summer, and those with spine deficiency were near shore.

Spatial and temporal regularity of some of the predators allow inferences on sources of mortality among different age, sex, and spine phenotypes. The major predators in open water are the common loon in spring and summer and the red-necked and horned grebes in winter. Dorsal and pelvic spines have been considered defensive adaptations to vertebrate predators in a number of studies on gastropods (Hagen and Gilbertson 1972; Moodie 1972; Hoogland *et al.* 1957). The prevalence of spined phenotypes in the limnetic region, as well as the greater spine complement among females, may represent an adaptation to these avian predators.

Data on parasites in the stickleback (Reimchen, in preparation) is in agreement with the suggestion that females incur greater avian predation than males. *Schistocephalus solidus*, a coelomic cestode of *G. aculeatus*, is significantly more common in females; this parasite matures and reproduces in the gut of a piscivorous bird (Clarke 1954). Among males (excluding all fish with *S. solidus*) there is a higher incidence of the intestinal cestode, *Cyathocephalus truncatus*; in this species, the fish is the definitive host (Lester 1974).

To a large-billed predator such as the common loon, it is possible that spines on subadults would not provide a significant deterrent. However, the red-necked grebe and horned grebe, because of their smaller bill size and ability to use alternate prey items (Godfrey 1966), may create a selective

pressure in which spined phenotypes even among juvenile fish have a slight advantage.

Predation by the kingfisher, all on adult fish, occurred near shore, and coincided with the distribution of adult male stickleback. On first sight, selection should favour males with full spine expression, yet they were spine deficient in comparison with females. When a fish was captured, it was taken to shore and manipulated on a log or other perch. Unlike prey capture by loon or grebes, there was a minimal escape probability during final manipulation; if dropped, as was occasionally seen, the fish could be retrieved, as it usually fell to the ground. In this case, greater number of spines would not confer an advantage on the fish. However, it is not known how the presence or absence of spines influences escape probability during the initial stages of capture and transport of the prey.

The abundance of aeshnid nymphs in the lake and observations in aquaria indicate that odonates are a source of predation in summer on young-of-the-year fish. Assessment of the hunting techniques suggested, firstly, that spines are not a defense against aeshnid nymphs, and secondly, that they may represent a disadvantage to the fish. For many vertebrate predators, prolonged manipulation time due to greater numbers or size of spines increases the probability of escape by the stickleback (see Wootten 1976). This occurs since the entire fish and erect spines are held within the mouthparts; spines can penetrate soft tissue leading to temporary release of the fish. Also, spines must be broken or depressed before swallowing is possible, leading to further manipulation. For aeshnid nymphs, the mouthparts do not usually encounter the spines when the prey is seized; initial capture is effected by labial palps which pierce and hold the body. As well, the presence of erect spines does not influence swallowing; mandibles of these species are well developed for ripping and slicing (Pritchard 1965) and the fish is progressively ingested from the general position where the labial palps penetrated the body wall.

Crucial to the interpretation of spine deficiency is whether external structures are a disadvantage to the stickleback. Such a disadvantage was inferred from observing aeshnid nymphs grip and restrain the struggling fish with its forelegs. This type of manipulation in which the legs are used for capture and restraint of prey occurs in several other groups of large invertebrates, including hemipterans and coleopterans (Hay 1974; Reist 1978). In the present study, predation experiments have not detected any disadvantage to spined phenotypes. Because of the efficiency of the aeshnid predator, a proper test

of the hypothesis would require considerably larger numbers of fish than were used. I observed only 2 out of 80 attacks in which the stickleback struggled free of the larva. If this proportion is representative, 6 individuals of the 390 used in the experiment would represent "escaped" fish (2.5% of 235). Even if these six individuals had been recognized and isolated from unattacked fish, with this number it would be possible to detect only exceptionally high selective coefficients. If least spined phenotypes have a small advantage, for example, 5%, over greater spined fish, the experimental design would require approximately 50 000 fish to detect selective mortality (i.e., contingency test).

Until such experiments are carried out, support or rejection of the hypothesis is dependent on a habitat correlation between macroinvertebrates and spine deficiency. In Boulton Lake, *Aeshna* was abundant in the littoral region, coincident with the distribution of fry (5–15 mm), all without spine expression, phenotypes of both sexes without a pelvis, and males, which are less spined than females (including occasional loss of third dorsal and anal spines). Spined phenotypes, in contrast, even among juveniles were most prevalent in the limnetic region where *Aeshna* was rare.

In the Paxton Lake population of *G. aculeatus*, Larsen (1976) detected behavioural and habit differences between "spined" and "non-spined" phenotypes. The former were primarily limnetic and fed on by salmonids; the latter were benthic, common in vegetation, and near lake bottom cover such as sunken logs. Although the influence of invertebrates as predators was not examined, aeshnid nymphs were common in the littoral habitat of "non-spined" phenotypes (J. D. McPhail, personal communication).

Among populations of *C. inconstans*, phenotypes with full pelvis were frequent in habitats without vegetation; those lacking the pelvis were common in areas of dense vegetation (Reist 1978). In the latter habitat, there was evidence for predation on juvenile stickleback by *Aeshna*, *Dytiscus*, *Lethocerus*, and northern pike, *Esox lucius*. In behavioural experiments, spine-deficient individuals maintained a greater distance from *Lethocerus* than fully spined phenotypes, and thus were less vulnerable to attack. For such behavioural adaptations to develop, a selective source of mortality by these invertebrates is implicated.

One characteristic of spine-deficient populations is the absence of predatory fish (Nelson and Atton 1971; Bell 1976; Moodie and Reimchen 1976b; Nelson 1977). On the Queen Charlotte Islands, these populations occur in bog pools and lakes which are

small and shallow, often with intermittent or closed drainage; they lack suitable spawning and wintering habitat for salmonids (Moodie and Reimchen 1976b), yet contain appropriate foraging substrate, such as *Nuphar* stands and submerged logs, for macroinvertebrates. Five species of *Aeshna* are associated with the bog habitat in this region (Cannings and Stuart 1977). In lakes with predatory fish, odonates are restricted to littoral cover, as salmonids readily consume nymphs moving across open substrate (personal observation). Hence, the absence of predatory fish may allow greater densities of macroinvertebrates or an expansion of their littoral range of activity (von Ende 1979), resulting in an overlap with the habitat of juvenile fish (as in Boulton Lake).

Where inferences are possible on the occurrence of macroinvertebrates, there is modest support for their relationship with loss of external structures such as spines. Further work requires information on the density of these invertebrates and the proportion of fish in their diet. In many treatments of morphological variation in gasterosteids, with notable exceptions of McPhail (1977), Nelson (1977), Bell (1978), and Reist (1978), the "absence of predatory fish" has been equated with the absence of predation. The result of this has been that alternate influences on mortality, and corresponding selective regimes, have been broadly neglected.

In Boulton Lake, age classes, phenotypes, and avian and odonate predators are not randomly distributed throughout the lake, and spine variation can, in part, be attributed to such differences. This tentative conclusion supplements current theoretical work on interpretation of phenotypic variation according to niche subdivision and environmental heterogeneity (Van Valen 1965; Gillespie 1974; Ewing 1979; Powell and Taylor 1979; Spieth 1979). More detailed assessment awaits a delimitation of the composite of habitats occupied by each phenotype and experimental data on capture techniques among different predators.

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